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Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects

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Ongoing climate change, as well as long-term overgrazing, is threatening biodiversity and ecosystem functioning in grasslands worldwide. Climate change and grazing could directly alter ecosystem functioning and stability, or indirectly by changing species diversity, composition and plant functional traits. By synthesizing results from publications of the most recent 30-years, we found that effects of climate change and grazing on biodiversity and ecosystem functioning varied from positive to negative, depending on different scenarios. Generally, aboveground net primary production (ANPP), belowground net primary production (BNPP), and species richness showed strong negative responses to 4°C warming, 50% precipitation decrease, and high grazing intensity. Responses of ANPP, BNPP and species richness to precipitation increase were mostly positive, whereas their responses to 2°C warming and low-to-moderate grazing intensity varied from positive to negative. Negative effects of 2°C warming on ANPP were substantially greater in grasslands that had been grazed than those that had not been grazed, and larger in arid and semi-arid grasslands than those in sub-humid and humid grasslands. Under 50% precipitation increase, ANPP responses were larger in grazed than ungrazed grasslands, and bigger in arid and semi-arid than sub-humid and humid grasslands. High levels of grazing intensity had greater effects on productivity and species richness than did warming and precipitation decrease. Currently, although there are increasing number of experiments which have included both climate change and grazing factors, more studies are needed to test the joint effects of climate change (e.g. warming, changes in precipitation patterns) and grazing (grazing intensity and livestock type) on biodiversity and multiple ecosystem functions. Multi-factor experiments would provide a more comprehensive understanding for sustainable grassland management in future.

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Introduction

Grassland ecosystems, covering about 40% of the earth's land surface and supporting nearly one-third of the global population, have experienced dramatic shifts in structure, species diversity and functioning driven primarily by climate change (e.g. warming and changes in precipitation patterns) [1–3,4•,5] and human disturbances (e.g. overgrazing) [6–8,9••]. For example, decreased precipitation, higher interannual variation in precipitation and warming could lead to a severe reduction in grassland productivity and carrying capacities for livestock [10,11]. However, experimental studies identifying the effects of warming, changing precipitation regimes, and grazing on species diversity, community structure, primary production and stability have generated contrasting or even controversial results [4•,7,8,12,13,14••,15•]. Thus, it is critical to get a better understanding of how climatic change, human disturbance (i.e. grazing), and biotic–abiotic interactions influence ecosystem structure, functioning and stability, and to provide guidelines for mitigating the impacts of climate change and improving adaptive grassland management.

Here, we provide a conceptual framework (Figure 1) to tease apart the direct effects of climate change and grazing on grassland ecosystem functioning and the indirect effects mediated by changes in community properties (i.e. species diversity, functional group composition and functional trait), based on hypotheses and predictions from ecological theories [16]. First, both climate change and grazing can directly affect ecosystem functioning by

Figure 1

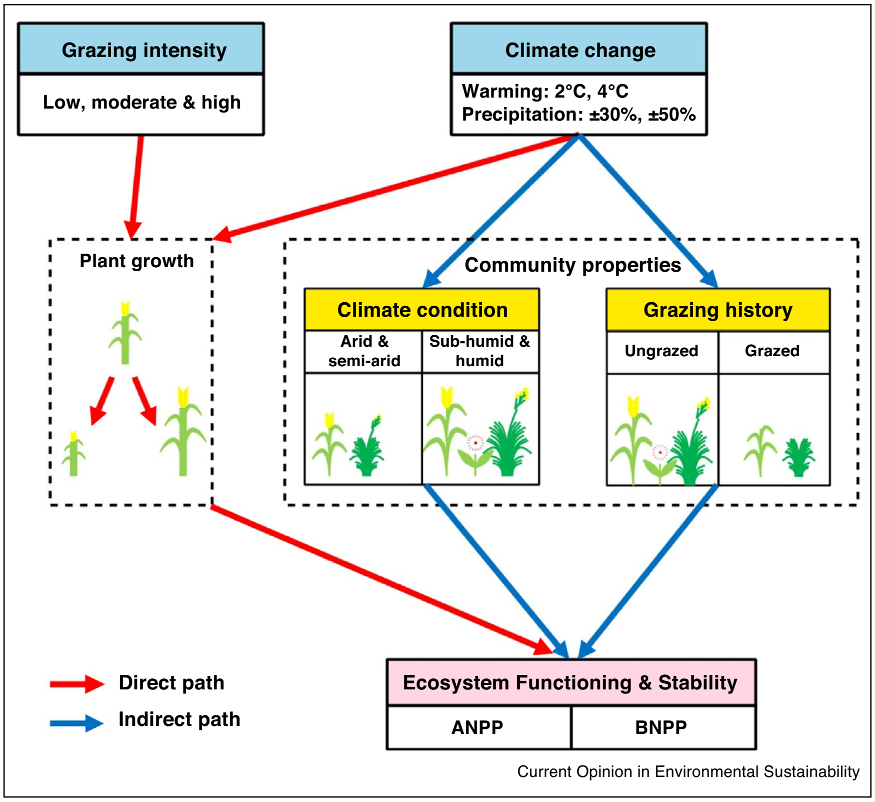


Diagram of the conceptual framework for this study. Direct effects of climate change (i.e. warming and changes in precipitation patterns) and grazing intensity on ecosystem functioning and stability and the indirect effects mediated by changes in community properties (i.e. species diversity, composition, functional traits and functional diversity).

regulating plant growth without changing species composition [17,18]. Second, climate change and grazing can indirectly affect ecosystem functioning through their influence on community properties [19,20]. Third, climate change and grazing effects on biodiversity and ecosystem functioning may also vary from arid to humid grasslands [5,9••]. One of the most fundamental properties of ecosystem functioning in grasslands is primary production, and both aboveground net primary production (ANPP) and belowground net primary production (BNPP) are controlled by multiple abiotic and biotic drivers [13,16,17,21]. Responses of productivity, stability and community properties to climate change and grazing could differ depending on scenarios of climate change and factors of grazing (Box 1). For example, global average surface temperature is projected to increase by 1.8–4°C by the end of the 21st century, and global average annual precipitation through the end of the century could increase or decrease by 30% to more than 50% in different areas [22]. Most grasslands are grazed under continuous or rotational regimes, mainly by domestic livestock, from low, moderate, to high grazing intensity (Box 1). To test these hypotheses and predictions, we synthesize results from publications of the most recent 30-years. Our study address three questions: first, how do ANPP, BNPP, species richness and stability respond to climate change variables (i.e. warming, precipitation increase and decrease) and grazing intensity (low, moderate and high) in grassland ecosystems? Second, how do the effects of warming, precipitation increase and decrease on ANPP, BNPP and species richness differ between grazed and ungrazed grasslands and under two contrasting climate conditions (i.e. arid and semi-arid versus sub-humid and humid)? Third, how do grazing and climate change variables interactively affect ANPP, BNPP, species richness and stability?

We collected data from published articles by searching the Web of Science, and used the following search terms to obtain papers from 1990 to 2017: (warming OR precipitation OR rainfall OR drought OR grazing OR livestock) AND (grassland OR dryland OR rangeland) AND (productivity OR ANPP OR BNPP OR stability OR diversity OR richness). To develop robust analyses, we only selected articles that meet the following requirements: first, studies that at least included one response variable: ANPP or BNPP or plant species richness; second, for climate change experiments, studies stated

Box 1 The key factors regulating biodiversity, primary production and stability in grassland ecosystems.

Climate change

IPCC reports that climate change is happening with global warming and changes in precipitation patterns [22]. From low emission to high emission scenario, temperature increases from 1.8 to 4°C are predicted by the end of 21st century [22]. Global average annual precipitation through the end of the century is expected to increase, but changes in the amount and intensity of precipitation will vary significantly by region. In semi-arid grasslands, precipitation is projected to decrease, and with less frequent, but more intense, precipitation events. Different experiments have increased or decreased precipitation amounts at multiple levels. Here, we divided treatments into four levels: −50% (including −50% or more), −30% (including −30% or less), +30% (including +30% or less), +50% (including +50% or more).

Grazing

Grasslands worldwide are dominated by grasses and shrub vegetation and controlled by precipitation, fire and grazing [67,68]. Grasslands are used for the production of domestic livestock, such as cattle and sheep. Continuous grazing and rotational grazing are two common practices: continuous grazing is a one-pasture system in which livestock have unrestricted access to the pasture throughout the grazing season; rotational grazing is a pasture system in which more than one pasture area is used and livestock are moved to different pastures during the grazing season [67,69]. We divided grazing intensity into light, moderate, or heavy treatments, depending on animal density.

Ecosystem functioning

Ecosystem functioning refers to the flow of energy and materials through the biotic and abiotic components of an ecosystem [70]. Grassland ecosystems that support livestock production and wild life provide numerous services, such as provision of food, fiber, water and genetic resources; climate and water regulation; support of soil formation; nutrient cycles; and as well as security and cultural services. Therein, net primary production is a crucial ecosystem function, including both aboveground net primary production (ANPP) and belowground net primary production (BNPP).

Ecosystem stability

Capacity of an ecosystem to persist in the same state. Five different aspects of stability are asymptotic stability, variability, persistence, resistance and resilience [71,72]. Asymptotic stability is a binary measure describing whether a system returns to the initial equilibrium after disturbances. Variability, the inverse of stability, is the coefficient of variation of a variable over time or across space. Persistence is the length of time a system maintains the same state before it changes in some defined way. Resistance indicates the ability to withstand the change. Resilience is the speed of recovery from change back to a former state.

Community properties

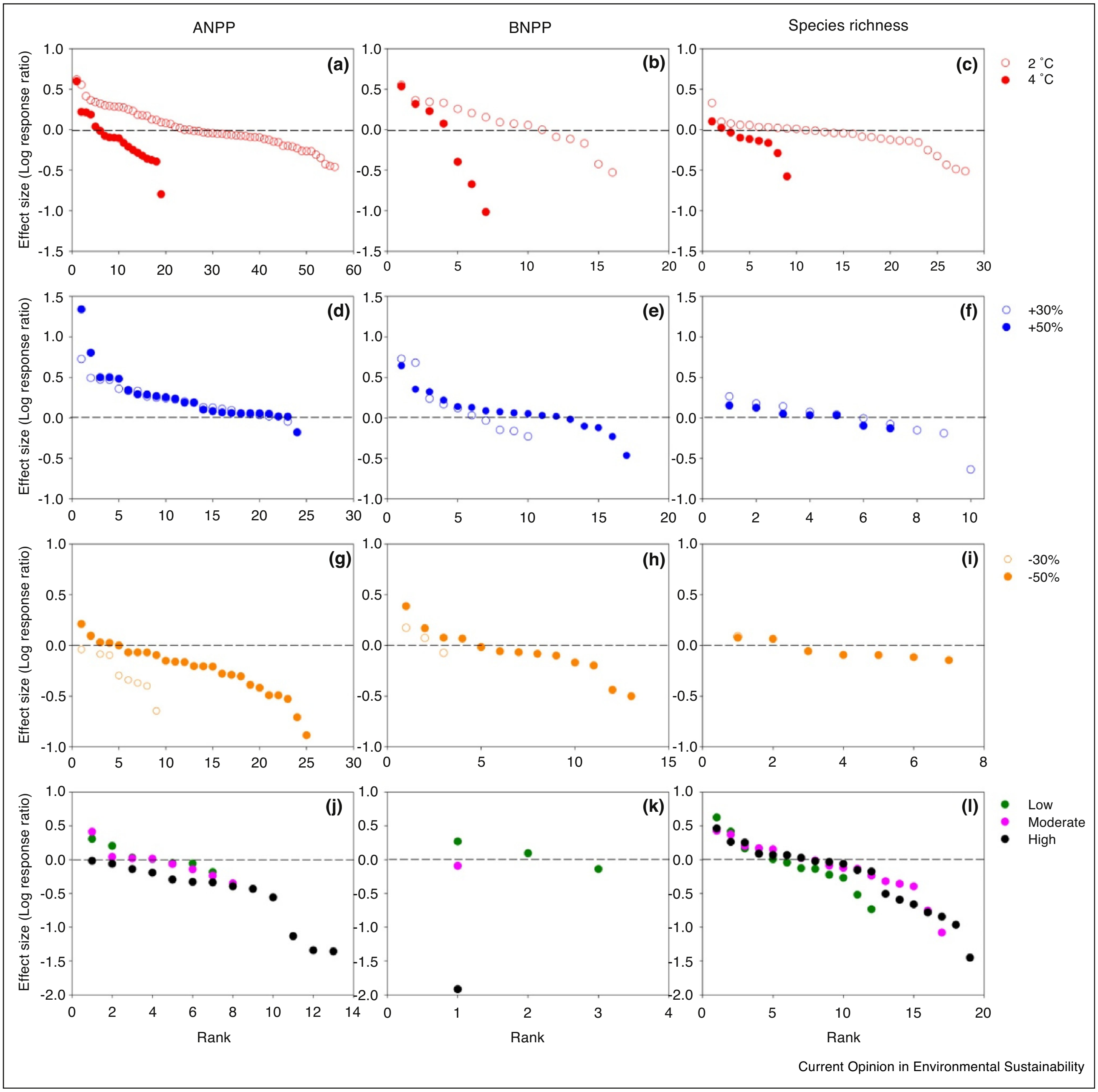
Communities have multiple components, including species diversity, functional group composition, and plant functional traits and so on. Classic species diversity measures include species richness, the Shannon–Wiener index and the Simpson index [73]. Species richness only depends on the number of different species, while the other two combine both richness and abundance. Functional groups or plant functional types are categories that define plants according to their function in ecosystems and/or their use of resources, for example, grasses, forbs and legumes. Plant functional traits are directly observable or measurable properties of plants that are related to how they respond to the environment or affect ecosystem functioning. Two community-level measures of plant functional composition are community weighted means (CWM) of traits and functional trait diversity. Functional diversity (FD) further includes four metrics: functional richness, functional evenness, functional divergence and functional dispersion [74].

whether the grasslands had been used for grazing before the start of experiments, and we did not include transplant experiments; third, for grazing experiments, at least one ungrazed plot and one grazed plot had been experimentally manipulated, and studies stated grazing intensity (low, moderate and high). Moreover, we only considered domestic herbivores. For multiple publications in a given experiment, each of these papers were included as a study. In total, our synthesis included 131 papers with 265 studies that have examined the independent effects of warming (90 studies), precipitation increase or decrease (101 studies), and grazing (74 studies) on ANPP, BNPP and species richness of grasslands, and 12 papers examined the joint effects of climate change and grazing. A list of the data sources was included in supplementary. We used OpenMEE to calculate log response ratio (RR) [23], which is the most widely used metric for measuring effect sizes in meta-analyses. RR is the ratio of mean in treatment group ($\overline{X}_e$) to that of the control group ($\overline{X}_c$) and converted to the metric of natural log [24]: $\ln \mathrm{RR} = \ln(\overline{X}_e) - \ln(\overline{X}_c)$. Then, we compared the responses of ANPP, BNPP and species richness to climate change factors and grazing intensity. Further, we compared the effects of climate change on these variables based on land use history (grazed or ungrazed before the start of experiment) and climate conditions. For climate conditions, we divided the experiments into two types of climate: arid and semi-arid versus sub-humid and humid, based on aridity index (AI), which is usually expressed as a generalized function of precipitation and temperature, and is a numerical indicator of the degree of dryness of the climate at a given location [25]. AI = MAP/MAE, where MAP is mean annual precipitation and MAE is mean annual potential evapotranspiration. Arid and semi-arid climate has AI = 0.03–0.5, and sub-humid and humid climate has AI > 0.5 [25].

Effects of climate change and grazing intensity on productivity, stability and community properties

Both 2°C and 4°C warming could increase ANPP and BNPP in many studies, which was consistent with findings from a meta-analysis that experimental warming generally stimulated plant growth and enhanced total net primary production [26••]. However, many studies showed that warming could decrease ANPP, especially at 4°C warming in which ANPP exhibited strongest negative response and reduced by up to 55% (Figure 2a). The negative effects of warming on ANPP could be directly resulted from reduced plant photosynthesis [27], and indirectly caused by reductions in resource availability and changes in plant community composition [28,29•]. For example, warming reduced soil N availability, and meantime, it reduced relative abundance of grasses but increased relative abundance of legumes [[26••]]. In addition, many studies showed that warming led to decrease in species richness (Figure 2c). Some researches

Figure 2



Log response ratios showing the impacts of warming, precipitation increase, precipitation decrease and grazing intensity on aboveground net primary production (ANPP), belowground net primary production (BNPP) and species richness. Each data point in a graph shows the effect of a climate change variable or grazing intensity on a response variable for one experiment, with experiments ranked by effect size.

proposed that not only species diversity, but also functional group composition and plant functional traits affected responses of productivity and stability to warming. For example, warming could either enhance ANPP and its temporal stability through promoting C_4 plant production [30•], or reduce stability of production by altering the temporal stability of dominant species and reducing the degree of species asynchrony [4•,31•]. Other studies found that effects of warming on productivity and stability were more dependent on community-weighted mean traits than diversity, because fast-growing species with higher specific leaf area, early flowering, erect growth habit, and rhizomatous strategy became dominant in warming treatments [32]. Compared to ANPP, 4°C

warming also decreased BNPP by up to 64%. Thus, a high degree of climate warming (e.g. 4°C) in the future may not be beneficial for the maintenance of species diversity and ecosystem functioning in grasslands.

Our meta-analyses showed that 30% and 50% precipitation increase had positive effects on ANPP, BNPP and species richness in most studies (Figure 2d–f). This was particularly true for ANPP; in almost all studies, ANPP showed positive responses to precipitation increase. For 50% precipitation increase, ANPP increased by up to 282%, compared to control. A recent global meta-analysis also found that water addition increased aboveground biomass [33]. Positive responses of productivity to increased precipitation could have resulted from direct effects of soil moisture on plant water status and photosynthesis [34]. In addition, responses of productivity could be regulated by different functional groups. For example, ANPP responses to water addition were mainly attributed to an increase in biomass of forbs [33]. Further, sensitivity of dominant species could also determine the magnitude of ANPP responses to altered precipitation amount [1]. However, the magnitude of responses in species richness and BNPP to precipitation increase was smaller than that of ANPP, and some studies showed that BNPP and species richness even declined under precipitation increase (Figure 2d–f). Two reasons might be responsible for decreases in BNPP and species richness: first, water addition shifted plant competition from belowground to aboveground and light competition became dominant, leading to a reduction in biomass allocation to belowground; second, intensified aboveground competition could increase competitive exclusion and lead to reduction in species richness [35]. In addition to changes in precipitation amount, models predict that growing season rainfall events will become larger in size but fewer in number [36,37]. Some researchers found that fewer larger rainfall events increased ANPP relative to many small events, because larger events could lead to greater soil water content and likely permitted moisture penetration to deeper in the soil profile [3,5].

In contrast to precipitation increase, most studies showed that precipitation decrease could reduce ANPP, BNPP and/or species richness (Figure 2g–i). Compared to 30% precipitation decrease, 50% precipitation decrease had much stronger negative effects on ANPP, BNPP and species richness, because water is one of the most limiting factors of plant growth in grasslands, especially in arid and semi-arid regions [38]. Recent studies found that productivity was more sensitive to water additions than reductions [14••,26••]. Our meta-analyses support such findings, because, for a given precipitation alteration, the absolute response ratios of ANPP and BNPP were higher under water addition than water reduction (Figure 2d–i). In addition, we found that for both precipitation increase and decrease: ANPP responses > BNPP responses > species richness responses. For example, 50% precipitation decrease could reduce ANPP, BNPP and species richness by up to 59%, 39% and 14%, respectively. A study pointed out that even with no change in total rainfall quantity, increased rainfall variability could reduce ANPP in a C_4-dominated grassland [34]. Drought could also affect productivity and stability by changing species diversity or composition [38,39]. Recent studies showed that higher species richness could modulate the negative impacts of drought, but drought could reduce the relative abundance of grasses and drive decreases in ANPP [2,40]. However, fewer studies compared how functional traits respond to different scenarios of precipitation [20,41]. A recent study found that increased precipitation favored species with small seed size, short leaf life span and high leaf nitrogen concentration [41]. More studies are needed to consider the role of plant functional traits in regulating the effects of climate change on ecosystem functioning.

Low and moderate levels of grazing intensity could increase or decrease ANPP (Figure 2j). The positive responses of ANPP to grazing were consistent with predictions of the grazing optimization hypothesis that ANPP peaks at a moderate grazing intensity, by eliminating standing dead biomass [42], stimulating nutrient cycling [43], and compensatory growth of plants after defoliation [18]. Such positive effects could happen even under water stress conditions [44]. On the contrary, ANPP decreased by up to 74% under high grazing intensity (Figure 2j). Although species richness responded positively to grazing intensity in some studies, many studies showed that grazing had negative impacts on species richness; species richness decreased by up to 77% at high grazing intensity (Figure 2l). High grazing intensity had greater negative effects on species richness than did warming and precipitation increase and decrease (Figure 2). A recent meta-analysis also reported that the response of species richness and diversity to increasing stocking rate from moderate to high levels was negative [9••]. Generally, low to moderate grazing could increase species richness by lessening plant light competition and enhancing regeneration, whereas heavy grazing could reduce species richness by eliminating grazing-intolerant species from the species pool [45,46]. By altering species composition, grazing might affect productivity and stability. For example, grazing tends to reduce abundances of grasses, but increase abundances of forbs in North American grasslands [47,48•]. Two recent studies demonstrated that communities with higher functional diversity showed higher ecological stability under grazing [49,50]. However, grazing had strong selection for species with grazing-avoidance strategies, such as low stature, small leaves and low nitrogen content, and species with grazing-tolerance strategies, such as high specific leaf area and high leaf nitrogen content [[9••],20,51], hence selective grazing might reduce functional diversity as well as

stability. Compared to ANPP and species richness, only a few studies examined BNPP responses to grazing intensity. High grazing intensity also showed strong negative effects on BNPP, which reduced by up to 85% (Figure 2k). Thus, it is important to adopt a suitable grazing intensity to maintain biodiversity and ecosystem functioning in grasslands.

Effects of climate change on productivity, stability and community properties in grasslands with different grazing history and climate conditions

Negative effects of 2°C warming on ANPP were substantially greater in grasslands that had been grazed than those that had not been grazed before the start of warming experiment (Figure 3a). Further, positive effects of warming on BNPP were most frequently occurred in ungrazed grasslands, while 2°C warming could reduce BNPP by up to 41% in grazed grasslands (Figure 3b). The 2°C warming generally reduced species richness, particularly in ungrazed grasslands (Figure 3c). When data were categorized by climate conditions, the positive effects of 2°C warming on ANPP and BNPP were greater in sub-humid and humid grasslands than those in arid and semi-arid grasslands, while the negative effects of 2°C warming on ANPP were larger in arid and semi-arid grasslands than those in sub-humid and humid grasslands (Figure 3d, e). Compared to 2°C warming experiments, 4°C warming experiments were fewer. Based on available studies, 4°C warming showed strong negative effects on ANPP, regardless of grazing history and climate conditions (Figure 3g, j). In arid and semi-arid grasslands, 4°C warming reduced ANPP by up to 55% and species richness by up to 44% (Figure 3j). Thus, warming could be more detrimental to biodiversity and ecosystem functioning in grazed than ungrazed grasslands, and in arid and semi-arid than sub-humid and humid grasslands.

Both 30% and 50% precipitation increase generally had positive effects on ANPP, regardless of grazing history and climate conditions (Figure 4a, d, g, j). Under 30% precipitation increase, ANPP responses were similar between arid and semi-arid grasslands and sub-humid and humid grasslands (Figure 4d). However, under 50% precipitation increase, ANPP responses were greater in grazed than ungrazed grasslands, and larger in arid and semi-arid than sub-humid and humid grasslands (Figure 4g, j). The low responses in sub-humid and humid grasslands may be resulted from intensified nutrient limitation when water limitation is lessened [52]. Compared to precipitation increase, 30% precipitation decrease had negative effects on ANPP, particularly in ungrazed, sub-humid and humid grasslands (Figure 5a, d), suggesting that plants in sub-humid and humid grasslands are sensitive to water stress. Only a few studies examined responses of BNPP and species richness to 30% precipitation decrease. Similarly, 50% precipitation decrease also had negative effects on ANPP regardless of grazing history and climate conditions (Figure 5g, j). ANPP decreased by up to 59% under 50% precipitation decrease. BNPP reduction was greater in arid and semi-arid than sub-humid and humid grasslands (Figure 5k).

Multi-factor experiments considering joint effects of climate change and grazing

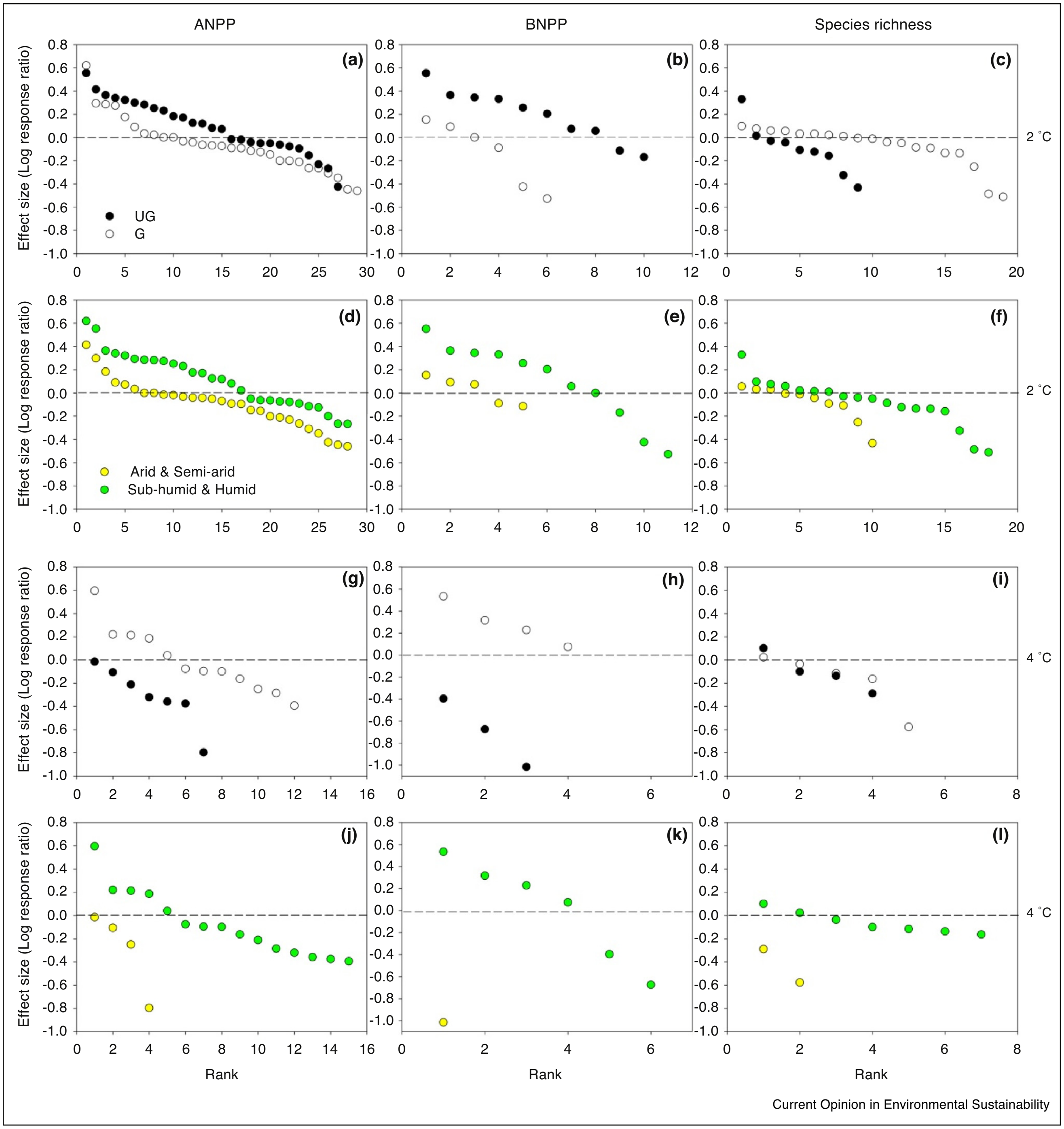
To get a better understanding of how climate change and human disturbance affect biodiversity and ecosystem functioning, multi-factor experiments are desirable to explore the interactions between climate change and grazing. Researchers have shown that although independent effects of simulated grazing (e.g. clipping) and warming on ANPP were negative in alpine meadow ecosystems [53], their combined effects could be positive [54]. In addition, drought reduced ANPP by 24% at high clipping frequencies (i.e. simulated high grazing intensity), whereas low clipping frequency (simulated low grazing intensity) was beneficial for the maintenance of ANPP under drought [55]. Moreover, combined warming and clipping could increase BNPP by 67%, while warming alone only increased BNPP by 42% [56]. The positive effects of combined warming and grazing could be resulted from their contrast effects on species composition. For example, warming and grazing had opposite effects on abundances of graminoids, legumes and forbs [12]; warming tended to increase shrubs but grazing could inhibit its growth [57]. In addition, warming could increase plant height but grazing could decrease it [58].

Similarly, grazing could exert stronger effects on plant growth in water limited areas [59], and warming, drought and simulated grazing had more negative effects on ANPP when grazing intensity was high [55]. However, water addition and simulated grazing can maintain total productivity [60]. Overall, both climate change and grazing are important drivers controlling biodiversity and ecosystem functioning in grasslands [61], they could reshape plant communities by altering the strength of intra-specific and inter-specific competition, which is critical to understand how plant species respond to global change [19].

Prospects

In the last 30 years, studies concerning climate change and/or grazing effects on grassland ecosystems have increased rapidly, especially those focused on climate change in recent years. However, few studies have explored how climate change drivers and grazing interactively affect biodiversity, ANPP, BNPP and ecosystem stability. Our meta-analyses indicate that the effects of climate change on biodiversity and ecosystem functioning were largely dependent on grazing history and climate conditions. Therefore, we highlight following aspects for future researches: first, more experimental studies are

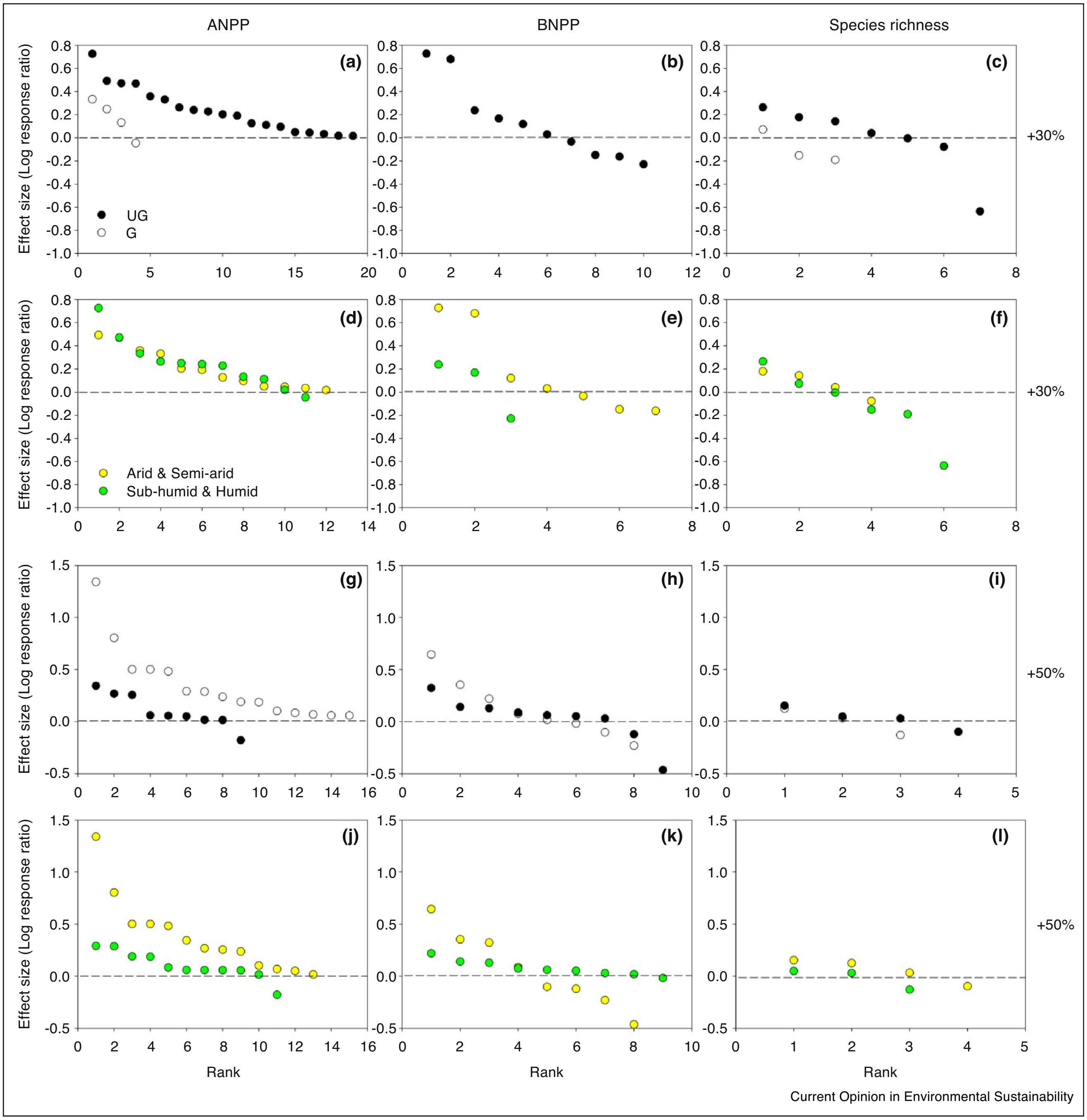
Figure 3



Log response ratios showing the impacts of 2°C and 4°C warming on ANPP, BNPP and species richness in ungrazed versus grazed grasslands, and arid and semi-arid versus sub-humid and humid grasslands. Each data point in a graph shows the effect of warming on a response variable for one experiment, with experiments ranked by effect size.

required to test how different scenarios of warming and changes in precipitation affect biodiversity, ecosystem structure, functioning and stability, which could provide a theoretical base for sustainable grassland management. Since responses of species diversity, ANPP and BNPP to climate change differ between arid and semiarid grasslands and sub-humid and humid grasslands, future studies should cover different climate conditions from arid to

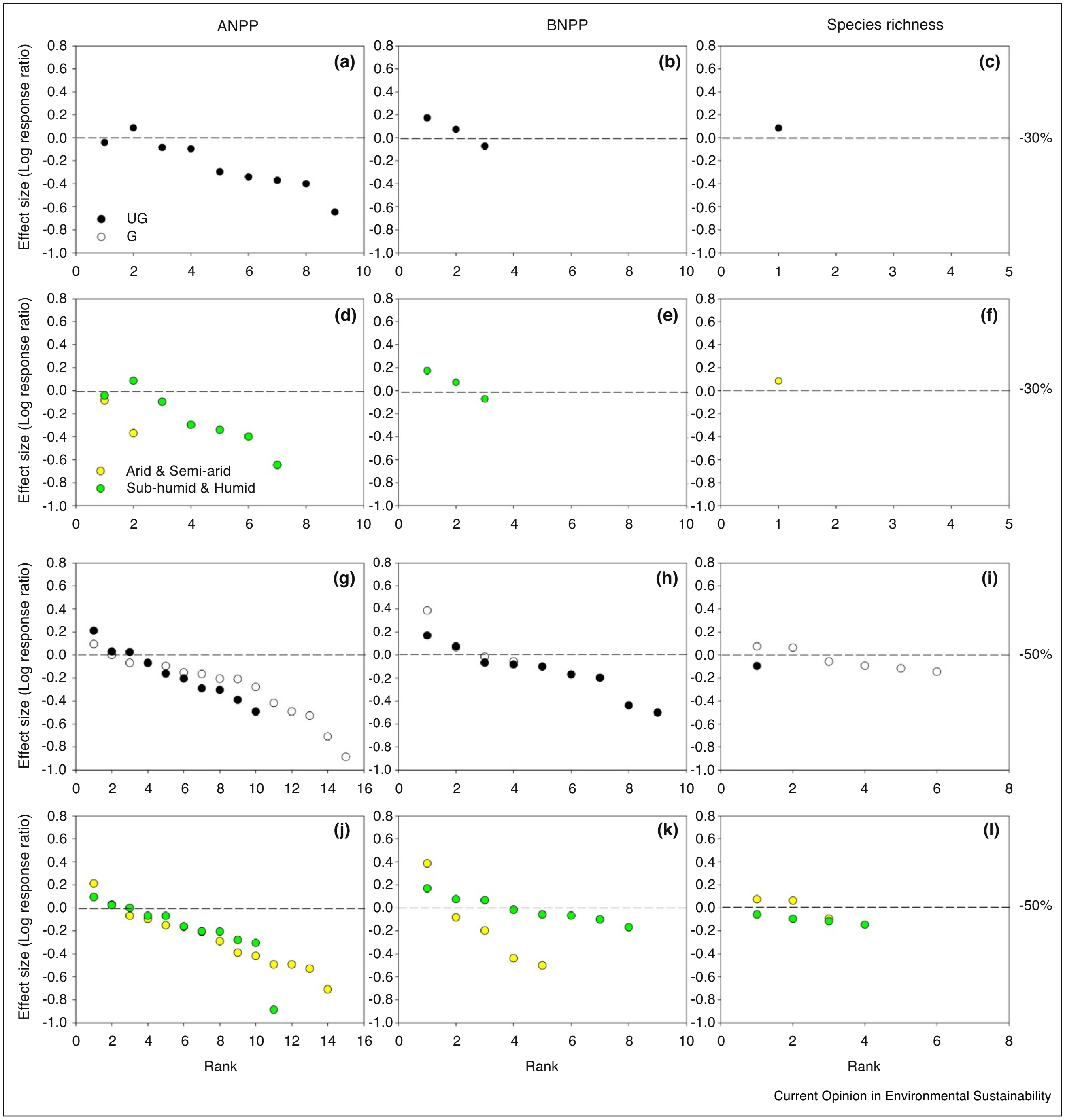
Figure 4



Log response ratios showing the impacts of 30% and 50% precipitation increase on ANPP, BNPP and species richness in ungrazed versus grazed grasslands, and in arid and semi-arid versus sub-humid and humid grasslands. Each data point in a graph shows the effect of a given precipitation increase on a response variable for one experiment, with experiments ranked by effect size.

humid regions. Second, experimental test of how climate change (e.g. day time versus night time warming, changes in precipitation amount and seasonality, extreme drought events) and grazing factors (e.g. type of grazing animals, continuous versus rotational grazing, and grazing intensity) interactively affect biodiversity and multiple ecosystem functioning and services. Third, more studies are needed to explore how changes in biodiversity and ecosystem functioning and services are mechanistically linked to alterations in functional traits, species

Figure 5



Log response ratios showing the impacts of 30% and 50% precipitation decrease on ANPP, BNPP and species richness in ungrazed versus grazed grasslands, and in arid and semi-arid versus sub-humid and humid grasslands. Each data point in a graph shows the effect of a given precipitation decrease on a response variable for one experiment, with experiments ranked by effect size.

composition and functional diversity [62–64]. Fourth, more researches should focus on how climate change and grazing affect belowground ecosystem properties (e.g. fauna, nematode, bacteria, and fungi community composition and diversity) and processes [65,66].

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.cosust.2018.05.008.

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- •• of outstanding interest

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